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#### SYSTEMATICS OF MILLER'S LONG-TONGUED BAT, *GLOSSOPHAGA LONGIROSTRIS*, WITH DESCRIPTION OF TWO NEW SUBSPECIES

WM. DAVID WEBSTER AND CHARLES O. HANDLEY, JR.

*Glossophaga longirostris* is a common nectar-feeding bat that occurs in northern South America and on some Caribbean islands as well. Despite its relatively wide distribution, few scientific collections contain a sufficient number of specimens from throughout its geographic range to permit an adequate evaluation of the variability in this species. Miller (1913*b*) examined 204 specimens of *G. longirostris* in his revision of the genus; he divided what he recognized as the "longirostris-group" into *G. l. longirostris* from coastal Colombia and Venezuela, *G. l. rostrata* from Grenada and the Grenadines, and *G. elongata* from Curaçao. More recently, Goodwin (1958) named and described *G. major* from Trinidad, but Koopman (1958) subsequently recognized it as a subspecies of *G. longirostris* and also arranged individuals from the Netherlands Antilles as *G. longirostris elongata*. Specimens from Boquerón de San Francisco (*ca.* Bogotá), Colombia, originally described by J. A. Allen (1916) as *Glossophaga apolinari* and listed by Cabrera (1958) as *Glossophaga longirostris apolinari*, actually represent *Anoura geoffroyi* according to Sanborn (1933) and our own observations, and they are not discussed beyond. Four subspecies of *Glossophaga longirostris* currently are recognized (Jones and Carter, 1976): *G. l. longirostris* from northern Colombia and Venezuela; *G. l. elongata* from Aruba, Curaçao, and Bonaire; *G. l. major* from Trinidad and Tobago; and *G. l.*

*rostrata* in the southern Lesser Antilles, from Grenada northward to St. Vincent.

A significant number of specimens of *G. longirostris* have been collected in the years since Miller's revision, the most noteworthy additions examined by us being those of the Smithsonian Venezuelan Project (SVP) (Handley, 1976) and the small but critical collection of O. P. Pearson from Huila, Colombia (deposited in the Museum of Vertebrate Zoology). These specimens allow us to assess the extent of geographic and nongeographic variation in *Glossophaga longirostris*, and to define better certain aspects of the biology that are poorly known in the species. This revision is based on the examination of 1188 specimens of *G. longirostris*, most of which are conventional skins accompanied by skulls; however, some consisted of skulls and postcranial skeletons, skulls without accompanying skins, or specimens preserved in fluid (from some of which the skulls had been extracted). All data on labels associated with specimens were recorded. Molt patterns were mapped for each individual found to have been in the process of molt. Measurements used in the morphometric analyses were taken from adults (completely fused phalangeal epiphyses and well-ossified cranial sutures) with dial calipers in millimeters; for definitions of cranial measurements see Handley (1959). Pelage coloration was assessed from individuals of *Glossophaga longirostris* deposited in the National Museum of Natural History under and Exam-O-Lite; color terminology from Ridgway (1912).

### *Glossophaga longirostris*

#### Miller's Long-tongued Bat

*Glossophaga longirostris* is known from northern South America (Colombia eastward to Guyana) and several of the Caribbean islands immediately adjacent to the mainland, including the Netherlands Antilles (Aruba, Curaçao, and Bonaire), the continental islands of Margarita, Trinidad, and Tobago, and the southern Lesser Antilles (Grenada, the Grenadines, and St. Vincent). Hummelinck (1940) reported *G. soricina* from the Testugos and several of the islands mentioned above. Some or all of these bats may represent *G. longirostris* (see Koopman, 1958), but Handley examined specimens of *G. soricina* from Isla Margarita in the SVP collections (Handley, 1976), Grenada (BMNH 67.5.4.5), and Bequia, Grenadines (BMNH 91.5.15.9).

### Diagnosis

Largest member of the genus in most external and cranial measurements; upper incisors noticeably and equally procumbent, I2 equal to I1 in bulk (occlusal view); P4 with reduced lingual cingular shelf; M1 narrow; parastyle of M1 usually absent or, if present, minute and directed posterolabially from paracone; mesostyle of M1 reduced, continuous with labial outline of tooth; fourth commissure of M1 long, well developed, and always longer than third; M2 similar to M1 except parastyle better developed, directed labially; lower incisors large and usually in contact, subtriangular in occlusal view, equal in bulk; p4 narrow, similar to p2 and p3 in bulk; premaxillae elongate anteriorly; pterygoid "wings" absent; presphenoid ridge usually high and complete throughout; mandibular symphyseal ridge absent, chin of mandible receding at a 45° angle; pelage bicolored, the tips of the individual hairs darker than the paler bases, Wood Brown to Fuscous dorsally, Avellaneous to Clove Brown ventrally; weight averaging 13.25 (10.3-16.0) grams in males, 12.81 (9.8-14.3) in nonpregnant females from throughout the range of the species.

### Comparisons

The morphology of the anterior region of the cranium and mandible in five species of *Glossophaga* is shown in Fig. 1. *Glossophaga longirostris* can be distinguished from *G. commissarisi* by its larger size in most external and cranial measurements. In addition, in *G. longirostris* the upper incisors are noticeably procumbent; the fourth upper premolar has a reduced lingual cingular shelf; the parastyle of M1 is absent or greatly reduced; the lower incisors are large, subtriangular in occlusal view, and usually in contact; the presphenoid ridge is high and complete throughout; the slope of the rostrum is not abrupt; and the mandibular symphyseal ridge is absent. In *G. commissarisi*, the upper incisors are not noticeably procumbent; P4 has a distinct posterolingual cingular shelf; parastyle of M1 is well developed; lower incisors are reduced in size and subcircular in occlusal view, with distinct gaps between the teeth; presphenoid ridge is flattened subterminally; slope of the rostrum is more abrupt; and mandibular symphyseal ridge is well developed.

Compared with *G. longirostris*, *G. leachii* is smaller in most external and cranial measurements. In addition, upper incisors are noticeably procumbent in *G. longirostris* (not noticeably procumbent in *G. leachii*), P4 has a reduced lingual cingular shelf (well



FIG. 1.—Incisor morphology in five species of *Glossophaga*. Oblique and dorsal view of the anterior rostral region (from top to bottom), and a dorsal view of the anterior mandibular region, in a typical specimen of, from left to right, *G. commissarisi*, *G. leachii*, *G. longirostris*, *G. mexicana*, and *G. soricina*.

developed in *G. leachii*), the lower incisors are large, equal in bulk, and usually in contact (small, unequal in size, the outer pair the larger, with gaps between the teeth, and usually arranged in two pairs in *G. leachii*); pterygoid “wings” are absent (present in *G. leachii*); facial profile is continuous from rostrum to braincase (abruptly dished facial profile in *G. leachii*); and mandibular symphyseal ridge is absent (well developed in *G. leachii*).

Specimens of *G. longirostris* can be distinguished from *G. mexicana* by larger size, both externally and cranially; presphenoid ridge high and complete throughout in *G. longirostris*, but flattened in *G. mexicana*; and mandibular symphyseal ridge absent in *G. longirostris*, but pronounced in *G. mexicana*. Canines and upper incisors are larger in *G. longirostris* than in *G. mexicana*. Lower incisors are large, usually in contact, and equal in bulk (occlusal view) in *G. longirostris*, but reduced in size, evenly spaced between the canines (outer pair the larger) in *G. mexicana*. In addition, in *G. longirostris* the mesostyle of M2 is greatly reduced, causing the labial outline of the tooth to be gently bowed outward at the parastyle and metastyle. The mesostyle of M2 in *G. mexicana* is well developed and the labial outline of the tooth is W-shaped.

*Glossophaga longirostris* can be distinguished from *G. soricina*, particularly in northern South America where they are sympatric,

by the larger dimensions of most external and cranial measurements. Pterygoid "wings" and mandibular symphyseal ridge are absent in *G. longirostris* (well developed in *G. soricina*), upper incisors are similar in bulk in *G. longirostris* (I2 smaller than I1 in *G. soricina*), lingual cingular shelf of P4 is reduced in *G. longirostris* (prominent in *G. soricina*), parastyle of M1 is absent in *G. longirostris* (well developed and directed anterolabially in *G. soricina*), mesostyles of M1 and M2 are poorly developed in *G. longirostris* (well developed in *G. soricina*), and p4 is narrow and similar to p2 and p3 in bulk in *G. longirostris* (p4 wider than p2 and p3 in *G. soricina*). Tamsitt and Valdivieso (1963) reported the noseleaf of *G. longirostris* to be smaller than that of sympatric *G. soricina* in central Colombia. Specimens of both species that we examined from the savannas of the Rupununi in Guyana and the llanos of Venezuela show the opposite relationship (specimens from each locality were collected on the same day and preserved in fluids in identical manner)—the noseleaf of *G. longirostris* averages 6.06 (5.7-6.4), whereas that of *G. soricina* averages 5.28 (4.6-5.7).

#### *Taxonomic Conclusions*

Patterns of geographic variation (Table 1) and a fragmented geographic distribution indicate that there are six subspecies of *Glossophaga longirostris*. Bats from the llanos of Venezuela and from low elevation grasslands around the Kanuku Mountains in Guyana represent an undescribed race that is relatively small in external and cranial dimensions, and has moderately large postorbital swellings. Specimens from Aruba, Curaçao, and Bonaire, to which the trinomial *Glossophaga longirostris elongata* Miller applies, are characterized by small measurements of the wing and a moderately long cranium that is narrow throughout. Bats from northern Colombia and northwestern Venezuela constitute another distinct race, *Glossophaga longirostris longirostris* Miller, that is moderately large in external and cranial dimensions, has reduced postorbital swellings, and a slightly dished facial profile. Another subspecies, *Glossophaga longirostris major* Goodwin, occurs along the xeric coast of Venezuela southward through the High Llanos of Colombia and Venezuela, and eastward to Trinidad. This race has a short and high braincase, dished facial profile, and inflated postorbital swellings. The disjunct population of bats in the upper Magdalena River Valley represents an undescribed subspecies that is distinguished by its massive size in

TABLE 1.—Selected measurements of six subspecies of *Glossophaga longirostris*; mean followed by two standard errors, sample size in parentheses, range in parentheses, and coefficient of variation.

Variate	Sex	<i>G. l. campestris</i> (Hato Cariben)	<i>G. l. elongata</i> (Curaçao)	<i>G. l. longirostris</i> (Guajira)	<i>G. l. major</i> (Isla Margarita)	<i>G. l. reclusa</i> (ca. Villavieja)	<i>G. l. rostrata</i> (Grenada)
Length of forearm	F	37.33±0.37(18) (35.9-38.7)2.11	37.68±0.89(5) (36.5-39.0)2.65	38.67±0.33(28) (37.0-40.3)2.23	38.18±0.35(37) (36.1-40.0)2.77	40.36±0.46(7) (39.5-41.4)1.51	38.41±0.39(17) (36.5-40.2)2.10
	M	36.90±0.22(38) (35.5-38.1)1.83	37.28±0.38(12) (36.1-38.3)1.77	38.05±0.31(36) (35.9-39.7)2.44	37.24±0.38(25) (35.0-38.9)2.61	39.44±0.50(8) (38.7-40.5)1.80	37.78±0.46(9) (36.6-38.9)1.81
Greatest length of skull	F	21.99±0.15(27) (21.2-22.7)1.75	23.49±0.26(8) (23.0-24.2)1.58	23.62±0.14(26) (23.0-24.2)1.50	22.63±0.20(23) (21.8-23.5)2.09	23.75±0.30(10) (23.0-24.4)2.02	22.01±0.14(14) (22.6-23.6)1.18
	M	21.86±0.11(65) (21.0-23.0)1.99	23.18±0.17(11) (22.7-23.6)1.19	23.37±0.13(34) (22.4-23.8)1.64	22.44±0.25(15) (21.4-23.2)2.16	23.62±0.25(9) (23.2-24.3)1.57	22.44±0.16(6) (22.2-22.7)0.81
Zygomatic breadth	F	9.58±0.11(65) (9.0-10.3)2.99	9.46±0.13(7) (9.3-9.8)1.82	10.22±0.10(15) (10.0-10.6)1.82	9.87±0.18(10) (9.3-10.2)2.91	10.23±0.20(10) (9.6-10.6)3.06	9.76±0.14(13) (9.3-10.2)2.66
	M	9.70±0.06(58) (9.3-10.2)2.16	9.37±0.17(11) (8.7-9.8)2.95	10.16±0.14(17) (9.4-10.6)2.93	9.91±0.15(9) (9.6-10.3)2.22	10.43±0.15(8) (10.1-10.7)2.03	9.88±0.14(6) (9.7-10.1)1.74
Breadth of braincase	F	8.74±0.07(29) (8.4-9.1)2.04	8.63±0.08(8) (8.5-8.8)1.35	9.07±0.06(27) (8.8-9.4)1.61	8.88±0.06(28) (8.6-9.2)1.72	8.99±0.14(8) (8.7-9.3)2.18	8.85±0.08(12) (8.7-9.1)1.56
	M	8.78±0.04(67) (8.4-9.1)1.83	8.52±0.11(11) (8.3-8.8)2.22	9.10±0.07(36) (8.7-9.7)2.43	8.93±0.10(18) (8.5-9.3)2.42	8.99±0.11(9) (8.8-9.3)1.88	8.64±0.12(7) (8.4-8.8)1.88
	F	7.18±0.06(29) (6.8-7.5)2.33	6.78±0.13(8) (6.6-7.1)2.70	7.32±0.06(27) (7.0-7.6)2.25	7.12±0.06(28) (6.8-7.7)3.54	7.31±0.18(8) (6.8-7.7)3.54	7.15±0.08(13) (6.9-7.4)1.95

TABLE 1.—Continued.

Depth of braincase	M	7.25±0.05(64) (6.7-7.6)2.83	6.73±0.11(11) (6.4-7.0)2.75	7.32±0.05(36) (6.9-7.8)2.23	7.19±0.08(17) (6.8-7.5)2.30	7.42±0.10(9) (7.3-7.7)1.99	7.08±0.15(6) (6.8-7.2)2.58
	F	4.57±0.05(29) (4.3-4.9)3.06	4.63±0.05(8) (4.5-4.7)1.53	4.80±0.06(27) (4.5-5.1)3.00	4.64±0.05(28) (4.4-4.9)2.69	4.80±0.08(10) (4.6-5.0)2.78	4.73±0.06(12) (4.5-4.8)2.04
Postorbital breadth	M	4.56±0.04(67) (4.2-4.9)3.33	4.52±0.10(11) (4.2-4.7)3.54	4.75±0.04(36) (4.5-5.0)2.78	4.63±0.06(18) (4.5-4.9)2.55	4.86±0.08(9) (4.7-5.0)2.33	4.58±0.10(6) (4.5-4.8)2.55
	F	7.64±0.05(29) (7.4-7.9)1.73	8.08±0.14(8) (7.8-8.4)2.37	8.17±0.07(27) (7.8-8.5)2.30	7.86±0.08(25) (7.5-8.2)2.52	8.36±0.08(10) (8.2-8.5)1.51	7.92±0.09(13) (7.7-8.2)1.98
Length of maxillary tooththrow	M	7.50±0.05(67) (7.1-8.0)2.59	7.97±0.08(10) (7.7-8.1)1.57	8.02±0.06(34) (7.7-8.5)2.15	7.70±0.11(18) (7.4-8.3)2.92	8.32±0.14(9) (7.9-8.6)2.46	7.76±0.07(7) (7.6-7.9)1.26
	F	5.67±0.06(29) (5.4-6.0)2.72	5.99±0.08(8) (5.8-6.1)1.89	6.25±0.07(27) (6.0-6.5)2.71	5.88±0.06(26) (5.5-6.1)2.77	6.26±0.09(10) (6.0-6.4)2.16	5.78±0.09(12) (5.5-6.0)2.75
Maxillary breadth	M	5.68±0.04(66) (5.2-6.1)3.15	6.00±0.07(10) (5.8-6.1)1.75	6.14±0.06(35) (5.8-6.5)2.91	5.87±0.10(18) (5.5-6.1)3.44	6.28±0.09(8) (6.1-6.5)2.04	5.82±0.14(6) (5.6-6.0)2.96
	F	3.87±0.05(29) (3.5-4.1)3.77	4.03±0.05(8) (3.9-4.1)1.76	4.13±0.06(26) (3.8-4.4)3.81	3.96±0.04(26) (3.8-4.2)2.38	4.30±0.07(10) (4.2-4.5)2.67	4.01±0.08(14) (3.7-4.3)3.76
Breadth across canines	M	3.94±0.03(66) (3.6-4.3)3.33	4.08±0.07(10) (3.9-4.3)2.79	4.28±0.04(35) (4.1-4.5)2.65	4.04±0.08(18) (3.7-4.3)3.99	4.49±0.06(9) (4.3-4.6)2.07	4.10±0.12(7) (3.8-4.3)3.98



external and cranial measurements and well-developed postpalatal processes. The insular populations that are known from Tobago and the Windward Islands from Grenada northward to St. Vincent represent another distinct race, *Glossophaga longirostris rostrata* Miller, that has a narrow rostrum, moderately reduced post-orbital swellings, a low and narrow braincase, and zygomata that converge anteriorly.

*Glossophaga longirostris campestris*, new subspecies

*Holotype*.—Adult female, skin and skull, no. 389033, U.S. National Museum of Natural History; from Hato San José, 20 km. W. Paragua (=146 km. S, 7 km. E Ciudad Bolívar), Bolívar Venezuela, 300 m.; obtained on 8 April 1967 by N. Peterson, D. Peacock, and R. Peacock, Smithsonian Venezuelan Project, original no. SVP 12679.

Selected external and cranial measurements of the holotype are: total length, 72; length of tail, 8; length of hind foot (dry), 12; length of ear from notch, 15; length of forearm (dry), 38.3; length of tibia (dry), 14.3; length of calcar (dry), 4.5; greatest length of skull, 22.2; zygomatic breadth, 9.6; breadth of braincase, 8.4; depth of braincase, 6.9; postorbital breadth, 4.6; length of maxillary toothrow, 7.6; maxillary breadth, 5.9; breadth across canines, 4.0; weight, 11.7 grams.

*Distribution*.—Llanos and Río Ventuari Basin of central Venezuela and savanna-clad lowlands around the Kanuku Mountains in Guyana and adjacent Brazil (Fig. 2); known altitudinal distribution from 50 to 300 meters.

*Diagnosis*.—For a *Glossophaga longirostris*, this subspecies is small both externally and cranially (Table 1). *G. l. campestris* is variable in cranial proportions, but on average the rostrum is short and narrow, braincase shallow and moderately low, facial profile moderately dished, and postorbital swelling moderately large.

*Comparisons*.—*G. l. campestris* can be distinguished from other subspecies by its small size and short, low braincase. Intergradation between *G. l. major* and *G. l. campestris* is evident in specimens from southern Guárico and northern Apure, Venezuela. The braincase of these bats is deeper and more bulbous (similar to *G. l. major*) than in typical *G. l. campestris*; however, they resemble the latter in having a short, narrow rostrum and in small overall size.



*Remarks.*—The isolated populations around the Kanuku Mountains suggests that *G. l. campestris* may be distributed discontinuously in suitable habitat throughout the Gran Sabana, especially along river valleys. However, it was not found at Icaburú at the southern edge of the Gran Sabana in Venezuela. Specimens of *G. l. campestris* have been collected from roosts in rock crevices, hollows of trees, and buildings. Pregnant females are known from December, and reproductively inactive females have been collected in April, June, and December.

The Latin epithet *campestris*, of or pertaining to fields or grasslands, refers to the preferred habitat of this race of *G. longirostris*.

*Specimens examined* (292).—BRAZIL. *Roraima*: Lucetania Ranch, 8 (ROM). GUYANA. *Rupununi*: Achimeriwau Mouth, 1 (ROM); "Bush Island," Dadanawa, 2 (AMNH); Chipirari Wau Mouth, 15 mi. E Dadanawa, 1 (ROM); Contanrib Island, 5 mi. above Dadanawa, 10 (ROM); 15 mi. ENE Dadanawa, 1 (ROM); 0-20 mi. E Dadanawa, 18 (2 AMNH, 16 ROM); Illia Wau River, 1 (ROM); Karanambo, 1 (AMNH); Kuitaro River, 5 (ROM); Mt. Tawatawun, ca. 8 km. E Dadanawa, 3 (ROM); Ruawau River, 30 mi. SW Dadanawa, 3 (ROM); Rock Cave, ca. Sand Creek Reservation, 5 (ROM); Sand Creek Village, 8 (ROM); "southern savannas," 17 (USNM); upper Sawariwau River, 7 (ROM); Wee Wee Tan, Makow Tan, 5 (ROM); Werí More, 4 (ROM). VENEZUELA. *Apure*: Hato Cariben, La Villa, 60 km. (=32 mi.) NE Puerto Páez, 76 m., 97 (USNM); Hato "La Guanota," 6 km. W San Fernando de Apure, 100 m., 1 (TCWC); Río Cinaruco, 41 km. NW Puerto Páez, 24 (USNM); ca. 4 km. W San Fernando de Apure, 66 m., 2 (TCWC); San Rafael de Atamaica, 45 km. S, 6 km. E San Fernando de Apure, 100 m., 7 (USNM). *Bolívar*: Hato La Florida, 14 km. S, 45 km. E Caicara, 50 m., 10 (USNM); Hato San José, 20 km. W La Paragua (=146 km. S, 7 km. E Ciudad Bolívar), 300 m., 10 (USNM); Isla de Cuba (Playa del Medio), Río Orinoco, 3 (UCV); Paso Caruachi, Río Caroní, 3 (UCV). *T. F. Amazonas*: Chaparito, 9 km. SE Puerto Ayacucho, 119 m., 6 (USNM); Coromoto, 25 km. SSE Puerto Ayacucho, 126 m., 1 (USNM); Guayaabal, 28 km. S Puerto Ayacucho, 135 m., 1 (USNM); Las Queseras, 12 km. SSE Puerto Ayacucho, 135 m., 4 (USNM); Morocoy, 65 km. SSW Puerto Ayacucho, 161 m., 3 (USNM); Paría, 25 km. SSE Puerto Ayacucho, 114 m., 2 (USNM); Puerto Ayacucho, 2 (UCV); 0.75 km. E San Juan, Río Manapiare, 1 (USNM); ca. 4 km. San Juan, Río Manapiare, ca. 163 km. ESE Puerto Ayacucho, ca. 155 m., 13 (USNM); Tamanaco, 4 km. NE San Juan, Río Manapiare, 155 m., 2 (USNM).

### *Glossophaga longirostris elongata* Miller

1900. *Glossophaga elongata* Miller, Proc. Biol. Soc. Washington, 13:124, 6 April.

1958. *Glossophaga longirostris elongata*, Koopman, Evolution, 12:437, December.

*Holotype.*—Adult female, skin (from specimen in alcohol) and skull, no. 101871, U.S. National Museum of Natural History; from Willemstad, Curaçao; obtained on 4 December 1899 by J. L. Guthrie, no original number.

Selected external and cranial measurements of the holotype are: total length, 65; length of tail, 6; length of hind foot (dry), 11;

length of ear from notch, 15; length of forearm (dry), 39.0; length of tibia (dry), 14.2; length of calcar (dry), 4.9; greatest length of skull, 24.2; zygomatic breadth, 9.4; breadth of braincase, 8.7; depth of braincase, 6.6; postorbital breadth, 4.7; length of maxillary toothrow, 8.4; maxillary breadth, 6.1; canine breadth, 4.0.

*Distribution.*—Aruba, Curaçao, and Bonaire (Fig. 2).

*Diagnosis.*—This insular subspecies is characterized by small measurements of the wing, an extremely narrow but moderately long cranium, and an exceedingly low braincase (Table 1). The postorbital swellings are reduced and the facial profile is flat or slightly concave rather than noticeably dished as in other races of *G. longirostris*. In addition, the zygomata of *G. l. elongata* are swept back in linear fashion rather than being flared as in specimens from the adjacent mainland.

*Comparisons.*—*G. l. elongata* can be distinguished easily from other races because it is larger than average for the species in measurements of cranial length, but smaller than average in measurements of the wing and cranial breadth.

*Remarks.*—Bats from the three Dutch islands exhibit variation in cranial dimensions, but the differences among them (based on small samples from Aruba and Bonaire) are not as great as between the islands and the mainland. Island and mainland populations are not so different, however, that occasional specimens are indistinguishable. The holotype of *G. l. elongata* is the largest of the series from Curaçao, and its flat facial profile does not resemble that of any individual from the mainland.

Some individuals have been collected from caves and rock fissures, and others have been taken in mist nets set over water (Miller, 1900*b*; Genoways and Williams, 1979). Nine females captured in February evinced no reproductive activity; however, volant young, subadult, and adult specimens were collected in August, indicating the recent termination of a reproductive cycle (Genoways and Williams, 1979).

*Specimens examined* (44).—NETHERLANDS ANTILLES. *Aruba*: Quaridikiri Cave, 1 (AMNH); no locality, 4 (USNM). *Bonaire*: Bolivia Dist., 2 (AMNH); no locality, 1 (USNM). *Curaçao*: NW end of island, 6 (USNM); Round Cliff, 1 (AMNH); Savonet, NW Willemstad, 10 (5 AMNH, 5 USNM); SW side of island, 3 (USNM); Willemstad, 8 (USNM); no locality, 8 (2 AMNH, 2 BMNH, 1 FMNH, 3 USNM).

Additional distributional records of *G. l. elongata* in the Netherlands Antilles are in Hummelinck (1940), Wille (1954), Husson (1960), and Genoways and Williams (1979).

*Glossophaga longirostris longirostris* Miller

1898. *Glossophaga longirostris* Miller, Proc. Acad. Nat. Sci. Philadelphia, 50:330, 25 July.

*Holotype*.—Adult female, skin and skull, no. 8046, Bang's Collection, Museum of Comparative Zoology, Harvard University; from Santa Marta Mountains (near Santa Marta), Colombia; obtained on 10 February 1898 by W. W. Brown, Jr., original no. 60.

Selected external and cranial measurements of the holotype are: total length, 80; length of tail, 18; length of hind foot, 10; length of ear from notch, 14; length of forearm (dry), 39.5; condylobasal length, 21.8; zygomatic breadth, 10.2; mastoid breadth, 9.8; interorbital breadth, 4.3; length of maxillary toothrow, 8.1.

*Distribution*.—Northern Colombia and northwestern Venezuela (Fig. 2); known altitudinal distribution from sea level to approximately 615 meters.

*Diagnosis*.—This moderately large race (Table 1) is characterized by a long stout rostrum, long low braincase, reduced postorbital swellings, and a moderately flat facial profile. An increase in size in external and cranial dimensions from southwest to northeast is evident; specimens from Península de la Guajira (Colombia) and Península de Paraguaná (Venezuela) are the largest in the cline, whereas those from Cartagena (Colombia) and Agua Santa (Venezuela) are the smallest.

*Comparisons*.—The large size, low braincase, and flat facial profile distinguish *G. l. longirostris* from other subspecies except the isolated race from the upper Magdalena River Valley of Colombia. *G. l. longirostris* can be distinguished from the latter by its less globous and lower braincase, and poorly developed and nonfalcate postpalatal processes.

*Remarks*.—*G. l. longirostris* is known to use caves as daytime roosts (J. A. Allen, 1900). Specimens have been captured in mist nets near farm buildings and in gallery forest (Pirlot, 1964). Pregnant and lactating females have been taken in June in Venezuela. Specimens in the process of molt also have been collected in June.

*Specimens examined* (296).—COLOMBIA. *Atlántico*: Barranquilla, 1 (FMNH); La Playa, 2 (AMNH). *Bolívar*: Bahía de Cartagena, Fuerte de San Fernando, 2 (FMNH); Cartagena, 2 (USNM). *Guajira*: 114-121 km. N, 25-32 km. W Maracaibo (Venezuela), 15-50 m., 27 (USNM); Valledupar (=Magdalena), Villanueva, 274 m., 5 (USNM). *Magdalena*: Bonda, 50 m., 5 (4 AMNH, 1 USNM); Mamatoco, Santa Marca [Marta], 15 m., 3 (CMNH); Minca, 600 m., 1 (USNM); Santa Marta Mountains (near Santa Marta), 1 (MCZ); Taganga, 0 m., 29 (26 AMNH, 2 CMNH, 1 USNM). *Sucre* (=Bolívar): Tolúviejo, 1 (USNM). VENEZUELA. *Falcón*: Cabo San

Román, Península de Paraguaná, 1 (UCV); Capatárida, 40 m., 116 (USNM); 48-49 km. N, 33-46 km. W Coro, Península de Paraguaná, 13-615 m., 36 (USNM); 20 km. S, 98 km. E Maracaibo, Hda. Socopito, 480 m., 1 (USNM); Río Tocuyo, 500 m., 5 (AMNH). *Lara*: 10 km. N El Tocuyo, Caserio Boro, 5 (USNM). *Trujillo*: 23 km. NW Valera, 90-95 m., 12 (USNM). *Zulia*: Maracaibo, 1 (FMNH); 110-114 km. N, 25-28 km. W Maracaibo, 5-15 m., 40 (USNM).

*Additional records*.—COLOMBIA. *Guajira*: Maicao; Riohacha (Morales-Alarcón *et al.*, 1968). VENEZUELA. *Lara*: Guárico (J. A. Allen, 1911). *Zulia*: Hda. El Cerro, ca. Rosario, Río Palmar (Pirlot, 1964).

[After the typescript for this paper was prepared, we received a copy of Albuja's (1983) synopsis of Ecuadorian bats, which included three coastal Pacific records for *G. l. longirostris* from that country.]

### *Glossophaga longirostris major* Goodwin

1958. *Glossophaga major* Goodwin, Amer. Mus. Novitates, 1877:5, 28 February.

1958. *Glossophaga longirostris major*, Koopman, Evolution, 12:438, December.

*Holotype*.—Adult female, skin and skull, no. 176288, American Museum of Natural History; from Ariapita Avenue, Woodbrook, Port of Spain, Trinidad; obtained in 13 June 1957 by M. Sookar, original no. 57-1200.

Selected external and cranial measurements of the holotype are: total length, 61; length of tail, 7; length of hind foot (dry), 13; length of ear from notch, 20; length of forearm (dry), 41.2; length of tibia (dry), 15.3; length of calcar (dry), 4.3; length of maxillary toothrow, 8.3.

*Distribution*.—Arid coastal areas of Venezuela, southward to the High Llanos of Venezuela and Colombia, and eastward to Trinidad (Fig. 2); known altitudinal distribution from sea level to approximately 305 meters.

*Diagnosis*.—This medium-sized subspecies is unusually variable in external and cranial measurements (Table 1). It is distinguished from other races by its short, high braincase; pronounced postorbital swellings; long, narrow rostrum; and noticeably dished facial profile. Variability is due, in part, to a cline in length of wing bones and depth of the braincase. Specimens from eastern Venezuela and Trinidad have large external measurements and an extremely high braincase, but toward the west, external measurements diminish and the braincase becomes shallower.

Intergradation with other subspecies also contributes to variability seen in *G. l. major*. Gene flow between this subspecies and *G. l. longirostris* is evident in populations from Boca de Yaracuy and Mirimire. In these specimens, the postorbital swellings are reduced, the facial profile is less abrupt, and the cranium is longer, but in other respects these bats agree with *G. l. major*.

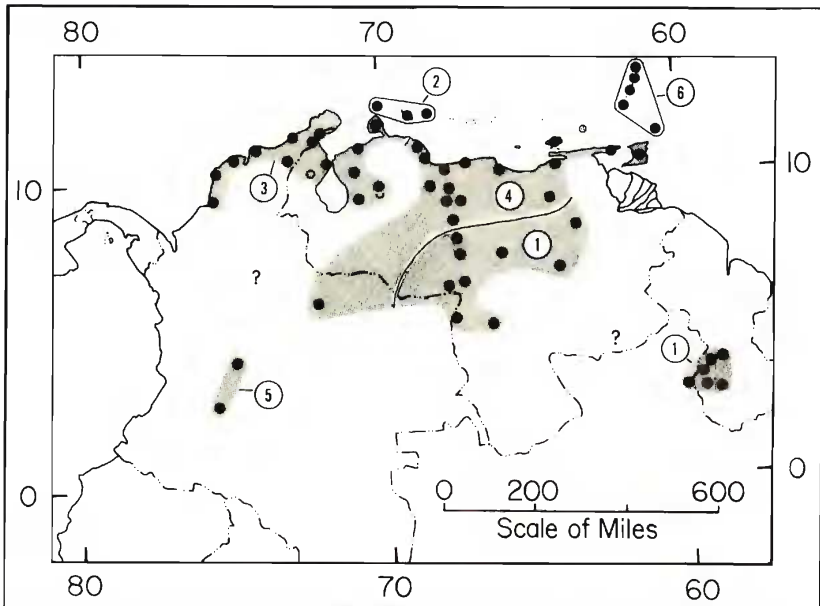


FIG. 2.—Geographic distribution of *Glossophaga longirostris* in South American and the Caribbean based on localities from which specimens were examined (solid circles) or reported in the literature (open circles): 1, *G. l. campestris*; 2, *G. l. elongata*; 3, *G. l. longirostris*; 4, *G. l. major*; 5, *G. l. reclusa*; and 6, *G. l. rostrata*.

*Comparisons.*—*G. l. major* is distinguished easily from other races by its domed braincase, concave facial profile, and pronounced postorbital swellings.

*Remarks.*—Known daytime roosts frequented by *G. l. major* include caves, houses, and buildings. It was found roosting with *Glossophaga soricina* at San Julián, Venezuela (Robinson and Lyon, 1901), and has been captured in mist nets in peach and mango orchards (Smith and Genoways, 1974).

Pregnant females have been taken in January, February, March, April, July, and August; lactating females are known from January, June, September, October, and December. Individuals in the process of molt have been collected in July, October, and November.

Pirlot (1965) recorded *G. longirostris* from Guayo, T. F. Delta Amacuro, Venezuela, but because we have not confirmed those identifications, we have not included that locality in Fig. 2. The xeric environments preferred by *G. longirostris* are not found in T. F. Delta Amacuro.

The skull of the holotype is badly broken and mended with glue. Goodwin (1958) noted that the "low braincase [of *major*]

suggest[s] a closer relationship with *elongata* than *longirostris* . . . ." Specimens of *G. l. major* from Trinidad examined by us have a high braincase, and we suspect that the damaged nature of the skull of the holotype may be responsible for the difference of opinion about braincase dimensions.

*Specimens examined* (380).—COLOMBIA. *Casanare* (=Boyacá): Pore, 1 (USNM). TRINIDAD. *St. George*: Gasparee Island, Gasparee Caves, 1 (OU); Port of Spain, 23 (14 AMNH, 1 LACM, 6 UMMZ, 2 USNM). *No locality*: 7 (1 FMNH, 6 UMMZ). VENEZUELA. *Anzoátegui*: Cantuara, 1 (USNM). *Aragua*: 1 km. S Ocumare de la Costa, 2 (USNM). *Carabobo*: San Esteban, 14 (8 AMNH, 6 BMNH). *Cojedes*: Galeras del Pao, 1 (UCV). *Distrito Federal*: Chichirivichi, 2 (UCV); La Guaira, 1 (USNM); Macuto, 3 mi. E La Guaira, 22 (2 AMNH, 1 FMNH, 1 MVZ, 18 USNM); Peña de Mora, 2 (USNM); San Julián, 8 mi. E La Guaira, 8 (1 MCZ, 7 USNM). *Falcón*: *ca.* Agüide, 19 km. N, 4 km. E Mirimire, 1-5 m., 20 (USNM); border with *Carabobo*, Boca de Yaracuy, 35 km. NW Puerto Cabello, 2 m., 14 (USNM). *Guárico*: Altagracia (de Orituco), 2 (FMNH); Calabozo, 100 m., 13 (USNM); Embalse de Guárico, 10 km. N Calabozo, 100 m., 19 (USNM); Estación Biológica de los Llanos, 12 km. S. 7 km. E Calabozo, 100 m., 1 (USNM); Hato Las Palmitas, 34 km. S, 12 km. W San Juan de los Morres, 181 m., 2 (USNM); Hato Masaguaral, 8 km. N, 2 km. W Corozo Pando, 100 m., 1 (TCWC); San José de Tiznados, 76 km. N, 16 km. W Calabozo, 150 m., 69 (USNM). *Miranda*: Hda. Bejuquero, S Río Chico, 1 m., 14 (USNM); 7 km. N Río Chico, 2 (USNM); 5 km. W Río Chico, *ca.* Puerto Tuy, sea level, 6 (USNM). *Nueva Esparta*: Cerro Matasiete, 2 km. N, 1 km. E La Asunción, 305 m., 32 (USNM); El Valle, 50 m., 7 (KU); *ca.* La Aguada, 3 km. S La Asunción, 53 m., 32 (USNM); 1 km. E La Guardia, 18 m., 1 (USNM); La Vencidad, 4 km. N, 8 km. W La Asunción, 19 m., 2 (USNM); Salamanca, 2 km. N, 1 km. E La Asunción, 38 m., 16 (USNM); 0.5 km. N San Francisco de Macanao, 75 m., 2 (KU); *ca.* Teatas de María Guevara, 2 km. N, 30 km. W Porlamar, 10 m., 1 (USNM). *Sucre*: 0-2.5 km. SE Cumaná, 10 m., 11 (KU); Ensenada Cauranta, 7 km. N, 5 km. E Güiría, 4 m., 4 (USNM); Isla de los Patos, 6 (2 AMNH, 1 FMNH, 3 MVZ); Quetepe, 16 km. E Cumaná, sea level, 7 (USNM); 5 km. E San Antonio del Golfo, 1 (KU); *ca.* Sotillo, 21 km. E Cumaná, 30 m., 10 (USNM).

*Additional records*.—TRINIDAD. *St. Patrick*: Point Fortin (Goodwin and Greenhall, 1961). VENEZUELA. *Aragua*: Cueva de Quebrada Honda (as *G. soricina*) (Linares, 1968). *Nueva Esparta*: Islas los Testugos, Isla de Conejo (Hummelinck, 1940).

### *Glossophaga longirostris reclusa*, new subspecies

*Holotype*.—Adult female, skin and skull, no. 113903, Museum of Vertebrate Zoology, University of California at Berkeley; from 4 km. E Villavieja, Huila, Colombia, 1400 ft.; obtained on 1 July 1950 by O. P. Pearson, original no. 3082.

Selected external and cranial measurements of the holotype are: length of head and body, 66; [length of tail, 0]; length of hind foot (dry), 12; length of ear from notch, 15; length of forearm (dry), 41.4; length of tibia (dry), 16.3; length of calcar (dry), 5.8; greatest length of skull, 23.7; zygomatic breadth, 10.0; breadth of



braincase, 8.9; depth of braincase, 7.4; postorbital breadth, 4.7; length of maxillary toothrow, 8.5; maxillary breadth, 6.3; breadth across canines, 4.2; weight, 13 grams.

*Distribution.*—Upper Magdalena Valley of Colombia at least from Cundinamarca southward to Huila (Fig. 2); known altitudinal distribution from approximately 325 to 500 meters.

*Diagnosis.*—This subspecies is large both externally and cranially (Table 1). The braincase is more globose, and the postpalatal processes are well developed and more falcate than those of the other nominal races. The dorsal pelage of *G. longirostris reclusa*, although bicolored and variable as in other taxa of *Glossophaga*, averages greater in contrast between the brownish tips and paler bases of the individual hairs than it does in other subspecies of *G. longirostris*, and is similar to that of *G. m. mexicana* of southern México (Webster and Jones, 1980).

*Comparisons.*—*G. l. reclusa* is distinguished from other subspecies by its large size and well-developed postpalatal processes. *G. l. reclusa* and *G. l. longirostris* are similar in several cranial dimensions that separate them from the other subspecies. The rostrum is long and stout rather than short and slender; the postorbital swellings are reduced; and the break in the facial profile (lateral view) is less obvious than that in populations to the east and south of the Cordillera de Mérida, but more dishd than that of *G. l. elongata*.

*Remarks.*—*G. longirostris reclusa* and *G. l. longirostris* are similar in cranial morphology and are distinguished primarily by differences in external and cranial measurements; the former exceeding the latter in most (Table 1). However, if *Glossophaga longirostris* is continuously distributed in the Magdalena Valley, then specimens from southern Bolívar, western Norte de Santander and Santander, and eastern Antioquia may be intermediate in size and a cline in body proportions may exist. We have not examined individuals that demonstrate gene flow between these races, but specimens have been reported from Santander (Morales-Alarcón *et al.*, 1968); these and other individuals from the Magdalena Valley should be compared for a better definition of the relationship between these two taxa.

Specimens of *G. longirostris reclusa* have been taken from culverts and small caves in the hot, semiarid Magdalena River Valley. They were found roosting with *Micronycteris megalotis* in a culvert near Villavieja and have been captured in the same mist net as *Glossophaga soricina* at Giradot (Tamsitt and Valdivieso, 1963; Valdivieso, 1964).



Pregnant females have been collected in June and July and a lactating female was taken in June. Two females captured in November evinced no reproductive activity. Specimens in the process of molt have been captured in November.

Although the holotype was recorded as not having a tail, the sheathlike portion of the uropatagium that enclosed the caudal vertebrae is clearly visible in that specimen, and the tail length averages 6.67 (range 4-10) in six other specimens from the vicinity of the type locality.

The Latin epithet *reclusa*, separated or removed, refers to the apparently disjunct nature of this population of bats in the upper Magdalena Valley.

*Specimens examined* (25).—COLOMBIA. *Cundinamarca*: 1 km. NE Giradot, 3 (AMNH). *Huila*: 5 km. N Villavieja, 1400 ft., 4 (MVZ); 4-7.5 km. E Villavieja, 1400 ft., 15 (MVZ); 17.5 km. SE Villavieja, 1600 ft., 3 (MVZ).

Records of *G. longirostris* from two localities in the upper Magdalena Valley of Cundinamarca (Mesitas del Colegio) and Tolima (Mariquita), as well as another in Meta (Villavicencio) on the eastern Andean slope, by Valdivieso and Tamsitt (1962) were not referred to in subsequent publications by the same authors (Tamsitt and Valdivieso, 1963; Valdivieso, 1964).

### *Glossophaga longirostris rostrata* Miller

1913. *Glossophaga rostrata* Miller, Proc. Biol. Soc. Washington, 26:32, 8 February.

1913. *Glossophaga longirostris rostrata* Miller, Proc. U.S. Nat. Mus., 46:423, 31 December.

*Holotype*.—Original description based on a specimen assumed to be an adult male (see below), skin and skull, no. 111500, U.S. National Museum of Natural History, from Westerhall Estate, Grenada; date of capture unknown ("1900"), obtained by P. Gelineau, original no. 29.

Selected cranial measurements of the holotype are: greatest length of skull, 22.6; zygomatic breadth, 9.8; breadth of braincase, 8.8; depth of braincase, 7.1; postorbital breadth, 4.8; length of maxillary toothrow, 8.0; maxillary breadth, 5.7; breadth across canines, 4.1.

*Distribution*.—Lesser Antilles from St. Vincent southward to Grenada (except Barbados), and Tobago (Fig. 2); known altitudinal distribution from sea level to approximately 625 meters.

*Diagnosis*.—External and cranial dimensions average in the middle of the range for the species (Table 1); larger overall on Tobago, smaller on St. Vincent. The rostrum is narrow, and the postorbital swellings are moderately reduced. The facial profile is moderately dished and the zygomata converge anteriorly.

*Comparisons.*—*G. l. rostrata* is distinguished from other races by its narrow rostrum and reduced postorbital swellings. The braincase is clearly less bulbous than that of *G. l. major* from Trinidad and northeastern Venezuela.

*Remarks.*—Handley and Webster (1985) argued that the holotype, selected by Miller from among the 14 specimens collected by P. Gellineau on Grenada in 1900, consists of a mismatched skin (a male) and skull (a female). They, therefore, restricted the holotype designation to the female skull, the male skin becoming a paratype. Furthermore, they noted that the purported date of collection, in fact, was the date that Gellineau mailed the specimens to the USNM, not the actual date of capture.

Specimens of *G. l. rostrata* have been taken from hollow trees in Grenada. They were found roosting with *Peropteryx macrootis*, *Micronycteris megalotis*, *Phyllostomus hastatus*, and *Carollia perspicillata* on Tobago (Goodwin and Greenhall, 1961). Pregnant females have been captured in August and December, and lactating females are known from March, June, and August. Individuals in the process of molt have been collected in August and September.

*Specimens examined* (151).—LESSER ANTILLES. Grenada: Grand Etang, 2000 ft., 5 (1 AMNH, 4 MCZ); Grenada, 1 (BMNH); Grenville Vale, 5 (AMNH); Pointe Saline, 3 (AMNH); 0-3.5 mi. NE St. George, 16 (6 KU, 9 MCZ, 1 TTU); St. Pauls, 4 (TTU); True Blue, 3 (AMNH); 0.5 mi. E Vendome, 1000 ft., 7 (1 KU, 6 TTU); Westerhall Estate, 14 (USNM); no locality, 7 (ROM). Grenadines: Carriacou, 23 (17 MCZ, 6 TTU); Mustique, 1 (BMNH); Union Island, 1 (MCZ). St. Vincent: Brighton, 8 (AMNH); Clifton Hill, 400 ft., 22 (KU); Grand Sable Estate, 7 (MCZ); Mesopatamia, 300 ft., 2 (KU); no locality, 4 (2 BMNH, 2 ROM). TOBAGO. Little Tobago: 2 (AMNH). St. Andrews: Orange Hill Rd., 3 (AMNH); Scarborough Government House, 3 (AMNH). St. David: Grafton, ca. Plymouth, 1 (LSU). St. John: 1 km. N Speyside, 5 (USNM). St. Mary: Pembroke, Gold Borough Estate, 1 (AMNH). St. Patrick: 1 km. SW Crown Point Airport, 3 (USNM).

Additional distributional records for *G. l. rostrata* from Grenada are in G. M. Allen (1911) and from Tobago are in Husson (1954).

#### BIOLOGICAL OBSERVATIONS

*Ecology.*—*Glossophaga longirostris* is a denizen of numerous lowland tropical and subtropical habitats in northern South America, including arid thorn forests, deciduous and evergreen forests, and savannas. In Venezuela (Handley, 1976), 837 individuals were collected within the following ecological parameters: site moisture—most frequently in dry areas (65 per cent) or near streams and other moist areas (35 per cent); habitat type—thorn forest (49 per cent), savannas and other open areas (43 per cent),

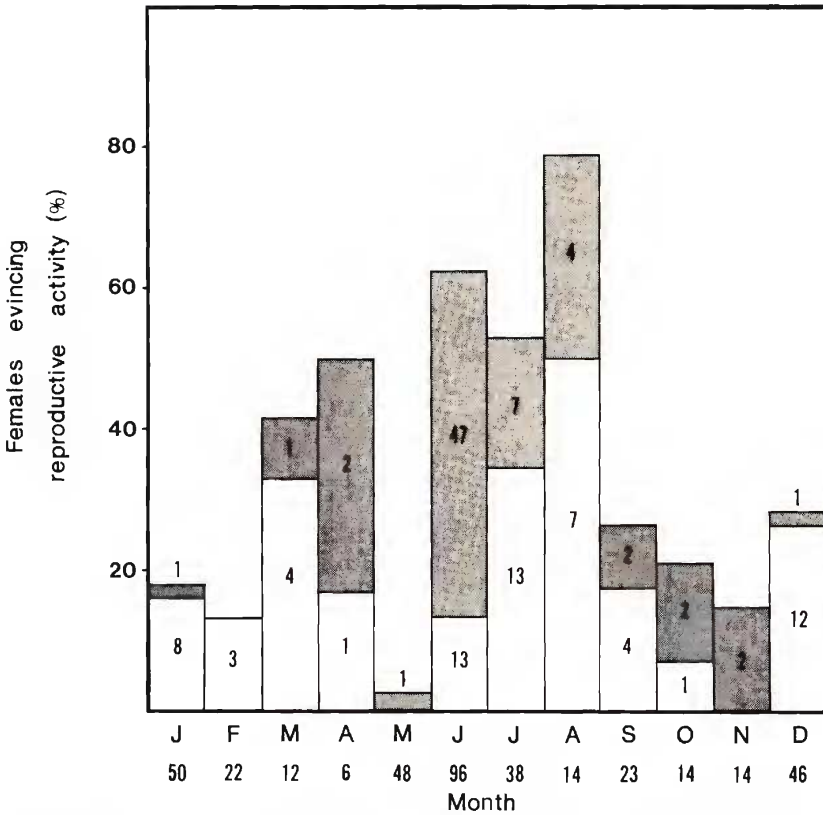


FIG. 3.—Reproductive activity in *Glossophaga longirostris*. The histogram represents the per cent of 383 females evincing pregnancy (open) or lactation (stippled) each month; the actual number of pregnant and lactating females is shown in the histogram, and the total number of females examined is below each month.

and moist forests (eight per cent); vegetative life zone—tropical dry forest (43 per cent), tropical thorn forest (35 per cent), tropical very dry forest (17 per cent), other dry zones (one per cent), and moist zones (four per cent). Daytime roosts include caves, tunnels, culverts, crevices in rocks, hollow trees, and houses and other buildings. Specimens have been captured from sea level to approximately 650 meters, but most are from less than 500 meters.

Other bats known to share daytime roosts with *G. longirostris* include *Peropteryx macrotis*, *Micronycteris megalotis*, *Phyllostomus hastatus*, *Glossophaga soricina*, and *Carollia perspicillata*.

*Reproduction.*—The reproductive condition of 383 females from throughout the geographic distribution of *Glossophaga longiros-*

TABLE 2.—*Timing of molt in Glossophaga longirostris based on the examination of 144 adult specimens.*

Month	Number examined	Number molting	% molting
January	18	0	0
February	4	0	0
March	12	0	0
April	2	0	0
May	1	0	0
June	26	4	15.4
July	15	2	13.3
August	23	4	17.4
September	5	1	20.0
October	9	1	11.1
November	9	3	33.3
December	20	0	0

*tris* was used to determine the percentage of pregnant and lactating females for each month (Fig. 3). Two periods of pregnancy are evident—one extending from December to April and another from June to October. Lactating females have been collected in every month except February. Thus, the reproductive strategy of *G. longirostris* appears to be that of monotocous polyestry with a bimodal cycle.

*Molt.*—Molt in adult *G. longirostris* occurs from June to November (Table 2), and appears to occur annually. The timing of molt is variable among specimens collected from the same place and at the same time and is not highly synchronized. A female from Isla Margarita (KU 118110) was pregnant while in the process of molt; therefore molt may not be delayed in reproductively active females in this tropical species as was found in *Eptesicus fuscus* in temperate North America (Jones and Genoways, 1967).

The sequence of molt in *Glossophaga longirostris* is similar to that of *G. soricina* (Jones *et al.*, 1973). Molt begins as a growth of new hair under the old. Then after the new fur has grown to half its normal length, the worn hair drops out in irregular patches rather than in symmetrical fashion. Generally, the hair on the head and shoulders is lost initially, but in some specimens hair on the back is replaced first.

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Addresses of authors: W. D. WEBSTER, *Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, Texas 79409*; C. O. HANDLEY, JR., *Division of Mammals, Smithsonian Institution, Washington, D.C. 20560*; Present address of WEBSTER, *Department of Biological Sciences, University of North Carolina at Wilmington, Wilmington, North Carolina 28403*. Received 7 September 1983, accepted 19 November 1984.